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Notes on Amphisbaenids (Amphisbaenia, Reptilia). 17 A Redescription and Discussion of *Amphisbaena angustifrons* Cope and *Amphisbaena camura* Cope of Southern South America

By Carl Gans[1]

INTRODUCTION

The systematic status of the two large species of *Amphisbaena* in southern South America has long been in a state of confusion. Five names (*angustifrons* Cope, *bolivica* Mertens, *boliviana* Werner, *camura* Cope, and *knighti* Parker) have been based on specimens of these two species, and individuals are identified by each of these names in various collections and reports. The types have never been re-examined, and our knowledge of these large and showy animals stems largely from comments on individual specimens in collections.

The present paper furnishes a standardized (Gans and Alexander, 1962) redescription of *Amphisbaena angustifrons* and *A. camura* based upon an examination, respectively, of 42 and 60 specimens, including all existing types. Material examined came from the collections of the following

[1] Research Associate, Department of Herpetology, the American Museum of Natural History; and Department of Biology, State University of New York at Buffalo, Buffalo, New York, 14214.

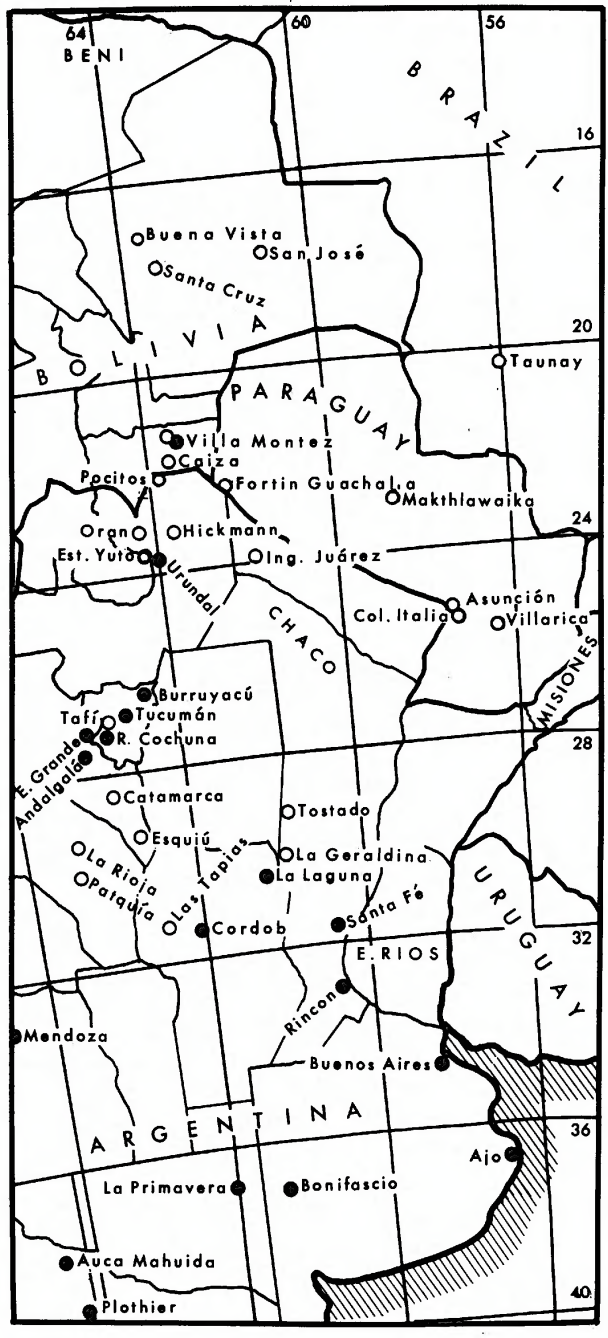

FIG. 1. Map of localities mentioned in text. Only those states for which specimens without more detailed locality were at hand have been labeled.

institutions (identified throughout by the abbreviations in parentheses), and I am grateful to those persons in charge of collections who lent the specimens employed in this investigation: the American Museum of Natural History, New York (A.M.N.H.); Academy of Natural Sciences of Philadelphia (A.N.S.P.); British Museum (Natural History), London (B.M.); Brigham Young University Collection, Provo, Utah (B.Y.U.C.); Carnegie Museum, Pittsburgh, Pennsylvania (C.M.); Chicago Natural History Museum, Chicago, Illinois (C.N.H.M.); Departamento de Zoologia, Secretaria da Agricultura, São Paulo, São Paulo, Brazil (D.Z.); Zoologisches Museum, Hamburg, Germany (H.M.); Instituto de Biología, Mendoza, Argentina (I.B.M.); Instituto Miguel Lillo, San Miguel de Tucumán, Argentina (I.M.L.); Museo di Zoologia della Universitá di Torino, Italy (I.M.Z.U.T.); Instituto Nacional Malbran, Buenos Aires, Argentina (I.N.M.); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (M.A.C.N.); Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy (M.S.N.G.); Museo Zoologíca dell'Universitá di Firenze, Florence, Italy (M.Z.U.F.); Naturhistorisches Museum, Basel, Switzerland (N.M.B.); Senckenbergische naturforschende Gesellschaft, Frankfurt-am-Main, Germany (S.M.F.); United States National Museum, Smithsonian Institution, Washington, D. C. (U.S.N.M.); Naturhistorisches Museum zu Wien, Austria (V.M.); Zoologische Sammlung des Bayerischen Staates, Munich, Germany (Z.S.M.). Mr. Eric Philips and Dr. Osvaldo A. Reig donated living specimens of *A. camura* and *A. angustifrons*. Dr. Virginia Cummings figured the specimens. Miss Kathleen Horton, Miss Charlyn Rhodes, and Mr. Mark Amdur furnished technical assistance. These studies are supported by N.S.F. G-21819 and GB-2460 from the National Science Foundation.

DISCUSSION

Discrimination of the Species

Even a cursory examination shows that the large amphisbaenids of Argentina, Paraguay, and Amazonian Bolivia represent two distinct forms differing from each other in color pattern, head shape, maximum size, number of segments to a midbody annulus (the number is high in both forms), and the arrangements of the segments. In addition, *Amphisbaena angustifrons* lacks caudal autotomy, while *camura* always has a clearly marked autotomy annulus at the fourth to sixth postcloacal caudal annulus.

There are no localities from which both are recorded, with the possible

exception of the immediate vicinity of Villa Montes, Tarija, Bolivia. The map (fig. 1) shows that *A. camura* ranges much farther northward into Amazonian Bolivia and Mato Grosso, Brazil, while the distribution of *A. angustifrons* extends southward into Neuquén. Both forms occupy an overlapping, but mutually distinct grouping of localities between latitudes 24° and 32° S. Both forms show geographical variation, but the trends are not parallel. The distribution suggests that the species are ecologically separated, but the nature of the separation is obscure. Both species seem to occur in montane and lowland situations.

Geographically the two species may replace the medium to large amphisbaenids *A. mertensi, A. fuliginosa,* and *A. alba* of central South America. It is pertinent, therefore, to comment on their differentiation vis-à-vis these morphologically distinct forms.

Amphisbaena mertensi (Gans, in press) is sympatric with *A. camura* at several localities in eastern Paraguay and possibly with *A. angustifrons* in Misiones (though records of the latter form from east of the Río Paraguay may be questionable). Paraguayan populations of *A. mertensi* are markedly smaller than either form, and also differ in head shape, color pattern, relative tail length, and numerous scale details.

Amphisbaena fuliginosa bassleri has recently been shown to extend south through the Bolivian Yungas (Rhodes, 1963). This lends credence to Serié's (1915) record for the "Chaco Austral," Argentina. The several forms are probably allopatric, but because of marked differences in their color pattern, and virtually all other characters examined, they appear to be distinct.

Amphisbaena alba has long been a catch-all name for large, more or less unicolored specimens with high numbers of segments to a midbody annulus. The species differs from *A. camura* in head shape, in the pattern of the meristic characters, and in the lack of caudal autotomy. The two species are apparently sympatric over a wide belt, since both have been taken at Buena Vista and San José (Bolivia), Taunay (Mato Grosso, Brazil), and in the vicinity of Asunción (Paraguay). While *A. alba* and *angustifrons* appear to be allopatric, they differ extensively in head shape, tail shape and proportions, and in the number of segments to a midbody annulus.

Assignment of Names

The type of *angustifrons* Cope (1861) was collected at Buenos Aires and deposited in the Academy of Natural Sciences of Philadelphia (A.N.S.P. No. 9690). Cope later (1885, p. 167, figs. 4a–4d) published a good, though diagrammatic, illustration of his unique specimen. In 1928 Parker

described *A. knighti* on the basis of British Museum specimens from a number of Argentine localities including Buenos Aires. The paper never mentions *A. angustifrons.* He was apparently misled by its relegation to synonymy as an abnormality by Ihering (1898, p. 104), as were Burt and Burt (1933, p. 78) and Amaral (1937, p. 199). Specimens in the type series of *A. knighti* are all typical *A. angustifrons.*

Amphisbaena camura was described by Cope (1862) on the basis of two specimens (U.S.N.M. Nos. 5860A, 5860B) from Paraguay. The specimens were obtained by an expedition that traveled up the Paraguay River and clearly belong to the east Paraguayan assemblage of *A. camura.* I therefore restrict the type locality to Asunción, Paraguay. In 1910 Werner inadequately described and did not illustrate *A. boliviana* from two specimens taken by Herman Ruschbach in the "Prov. Beni, Bolivia, Quellgebiet des Amazonas." The syntypes, apparently destroyed in 1944, were in the collection of the Zoologischen Museums, Hamburg. The meristic characters cited in his diagnosis (table 2) agree well with those of the Santa Cruz material of *A. camura,* but Werner's statement that the third "sublabial" of his specimens was the largest in the series does not fit. This may have referred to the distance of contact along the jaw edge rather than to absolute segment size. His failure to mention a light nuchal band may be explained by its absence or obscurity in some medium and large specimens from Bolivia. The name remains available for a north Bolivian population.

In 1929 Mertens described the new race *A. camura bolivica* on the basis of one complete and one incomplete specimen (S.M.F. Nos. 22099, 28705) collected at Villa Montes on the Río Pilcomayo in Bolivia. *Amphisbaena boliviana* Werner was not mentioned in the discussion. The name *bolivica* belongs in the synonymy of *A. camura,* but it is available for a south Bolivian population of that species.

Geographical Variation of *Amphisbaena angustifrons*

Examination of the data (table 1) indicates that the degree of character variation is probably inadequately characterized by the available samples. Specimens from Buenos Aires, Santa Fé, and Cordoba differ slightly from those from northwestern Argentina (and Bolivia) in the number of body annuli, means for the number of dorsal and ventral segments in midbody annuli, and the number of caudal annuli.

Clearly significant differences occur only in the southwest. Specimens from Mendoza and Neuquén have from 245 to 253 body annuli, while the number of those of the more eastern and northern specimens varies from 190 to 211. One Bonifascio specimen and the samples from La

TABLE 1

DATA FOR SPECIMENS OF *Amphisbaena angustifrons*

Collection and Number	Body, Lateral, and Caudal Annuli	Dorsal and Ventral Segments	Chin Segments	Labials	Cloaca	Total Length
M.S.N.G. No. CE —	203+3+17	27−8+25−6	2+5+12	4/3	4+8+15	257+28
M.A.C.N. No. 4166	207+4+16	22+26	2+5+11	4/3	5+7+16	292+25
M.A.C.N. No. 3760	199+4+12	22+24−5	2+5+9	4/3	4+7+16	345+36
M.A.C.N. No. 17843	207+4+14	25—6+30	2+5+13	4/3	4+8+15	243+19
M.A.C.N. No. 17856	202+4+15	27+26−7	2+5+12	4/3	4+6+15	339+35
M.A.C.N. No. 17859	209+4+15	31+30	2+6+11	4/3	4+8+14	342+33
M.A.C.N. No. 17879	199+3+15	26−9+27	2+5+11	4/3	4+9+14	263+26
M.A.C.N. No. 17881	199+3+15	28−9+27−9	2+7+12	4/(3)4	4+6+14	283+28
B.M. No. RR1946.8.8.71	203+2/3+15	20−3+27	2+4+10	4/3	4+7+14	293+28
B.M. No. RR1946.8.8.72	205+2/3+16	22+	3+5+12	4/3	5+	283+25
A.M.N.H. No. 17023	202+4/3+17	29+28−9	2+5+9	4/3	4+8+16	257+26
A.M.N.H. No. 65190	205+3+15	28+28	3+4+12	4/3	4+6+15	318+31
A.N.S.P. No. 9690	197+3+16	28+28	2+4+12	4/3	4+10+20	328+32
M.A.C.N. No. 6903	200+4+15	26+26−8	2+4+11	4/3	4+8+14	325+35
M.S.N.G. No. CE29010	203+4+17	23−4+25−7	3+5+10	4/3	4+7+16	322+38
B.M. No. RR1946.8.31.76	201+4+15	24+28	2+5+12	4/3	4+6+15	272+27
B.M. No. 1927.5.26.4	215+4+15	22−3+27	3+5+12	3+/3	4+6+18	313+29
M.A.C.N. No. 7916	223+4+17	20+24−5	2+5+11	4/3	4+6+14	268+25
M.A.C.N. No. 7917	210+3/4+16	23+24	2+5+10	4/3	4+6+15	197+20
M.A.C.N. No. 7918	220+3+17	27+27−8	2+5+12	4/3	4+8+13	235+25

TABLE 1—(*Continued*)

Collection and Number	Body, Lateral, and Caudal Annuli	Dorsal and Ventral Segments	Chin Segments	Labials	Cloaca	Total Length
M.A.C.N. No. 7976	253+4+18	24+26	2+5+12	4/3	4+8+14	223+22
M.A.C.N. No. 10262	250+4+18	22−4+24	2+6+14	4/3	4+8+13	217+22
M.A.C.N. No. 17878	245+4+18	24+30	2+5+10	4/3	4+8+16	273+26
U.S.N.M. No. 22764	212+3+16	23+28	3+5+10	4/3	4+6+12	260+23
C.M. No. 38031	214+3+18	24+24	3+4+?	4/3	4+6+17	281+27
H.M. No. 5220	209+4+16	25−8+28	3+5+14	4/3	3+8+14	271+28
M.A.C.N. No. 17875	205+3+15	24−6/27−8	2+5+12	4/3	4+8+12	292+29
M.A.C.N. No. 4346	214+3+16	22/23−4	2+5+9	4/3	4+6+16	269+25
M.A.C.N. No. 3586	211+3+15	22/26	3+5+10	4/3	4+6+12	103+9
M.A.C.N. No. 10893	190+3+13	20−1/26−8	2+10	3?/3	4+6+12	255+22
M.A.C.N. No. 10894	195+4+13	22−4/28−9	3+10	4/3	4+6+14	130+12
M.A.C.N. No. 10895	191+4+14	21−2/26	2+10	4/3	4+6+13	96+9
B.M. No. 1902.7.29.65	204+3+16	20−1+24	2+4+10	4/3	4+7+12	224+21
I.M.L. No. 148	196+4+15	23−4+30	2+5+11	3−4/3	4+8+14	285+29
I.M.Z.U.T. No. 967-A	208+3+15	26−7+29	—	4/3	5+6+16	301+27
M.A.C.N. No. 17860	195+4+13	22−3+25−6	2+(2)+10	4/3	4+8+14	268+24
I.M.L. No. 245	201+4+14	24−6+27−8	2+5+12	4/3	6+8+14	—
I.M.L. No. 199	197+3/4+15	20+20−2	2+3+8	4/3	4+6+14	192+18
I.M.L. unnumbered	207+3+14	20−2+29−31	2+5+11	4/3	4+7+14	~250+20
M.A.C.N. No. 17857	206+4/3+15	24+25−6	2+5+10	4/3	4+6+14	272+28
I.M.L. No. 143	191+4+13	23−4+25−6	2+(1)+9	4/3	4+8+15	220+19
Z.S.M. No. 228/33	196+3+14	24+24	2+4+[13]	3/3	4+8+15	252+23

TABLE 2

DATA FOR SPECIMENS OF *Amphisbaena camura*

Collection and Number	Body, Lateral, and Caudal Annuli	Dorsal and Ventral Segments	Chin Segments	Labials	Cloaca	Total Length
M.A.C.N. No. 4504	205+4+(5)22	32+29−30	2+5+10	4/3	4F+10+15	330+40
Z.S.M. No. 223/33	203+4+(5)x	30−2+30−2	2+5+10	4/3	4+ 8+16	330+x
M.A.C.N. No. 17451	207+3+(6)22	29+30	2+7+11	4/3	4+10+16	357+46
B.M. No. 1912.11.19.1	210+4+(5)26	29+29	2+5+0	4/3	4+?	338+63
M.A.C.N. No. 17876	204+3+(5)22	29+28	2+5+10	4/3	4+10+14	193+27
M.A.C.N. No. 17877	214+4+(5)23	29−30/29	2+4+13	4/3	4+10+14	242+35
M.S.N.G. No. CE 28311	202+3/4+(4)23	28+28	2+5+0	4/3	4+ 9+11	335+50
M.Z.U.F. No. 3217C272	208+4+(5)22	30+31?	—	—	4 —	362+33
M.A.C.N. No. 11915	208+3+(5)23	31−2+28−30	2+4+10	4/3	4+10+15	254+34
M.A.C.N. No. 11916	204+3+(5)22	28−9+29	2+5+10	4/3	4+10+13	302+39
M.A.C.N. No. 7970	207+3+(6)24	34−6+30−2	2+5+12	4/3	4+10+15	299+39
I.M.L. No. 56	208+4+(5)23	32−3+26−8	2+5+11	4/3	4F+ 9+17	346+49
M.A.C.N. No. 17822	209+3+(5)23	31+28−30	2+5+11	4/3	2−2+10+14	224+29
M.A.C.N. No. 17823	205+3+(6)23	30+28−30	3+6+13	4/3	4F+10+15	290+39
M.A.C.N. No. 17824	208+3+(5)22	30+20−30	2+5+12	4/3	4+ 8+14	292+38
M.A.C.N. No. 17825	206+3+(5)23	32−3+28−32	2+5+11	4/3	4+10+15	375+48
S.M.F. No. 11819	209+4+(5)x	28−30+30	2+5+10	4/3	4+ 9+14	285+x
I.M.L. No. 26	212+4+(5)x	33−4+33	2+5+12	4/3	4+ 8+16	388+x
I.M.L. No. 237	217+3+(5)19	31−2+32	2+5+11	4/3	6+10+16	274+36
I.M.Z.U.T. No. 1908	212+4+(4)18	35+35	2+5+13	4/3	6+ 9+15	406+43
I.M.L. No. 50	206+4+(6)25	32−3+32	2+5+12	4/3	4F+10+18	286+41
I.B.M. No. 60R	217+4+(6)20	32+30	2+5+11	4/3	4F+10+14	485+53
M.A.C.N. No. 17855	206+4+(4)x	38−9+44	2+5+11	4/3	4+11 —	324+x
N.M.B. No. 3812	199+4+(4)16	39+42	2+5+12	4/3	4+ 9+18	399+37
U.S.N.M. No. 5860A	200+4+(5)15	39+39	2+5+11	4/3	5+10+15	?380+37
U.S.N.M. No. 5860B	200+4+(4)15	42+42	2+4+10	(3)4/3	6+10+18	355+33
V.M. No. 12329	200+4+(4)15	39−40+46	2+5+12	4/3	5+10+18	304+30
A.M.N.H. No. 25173	194+3+(5)16	38+37	2+5+10	4/3	4+10+18	273+26
C.N.H.M. No. 42292	194+4+(5)16	40+40	2+5+11	4/3	4+ 9+18	360+35
B.M. No. 94.3.14.23	198+4+(5)16	35−7+38	2+6+12	4/3	4+10+20	408+39

B.M. No. 94.3.14.24	200+4+(5)17	36−7+45	2+5+10	4/3	4+11+15	374+35
B.M. No. 94.3.14.25	199+4+(4)15?	36−40+42	2+5+11	4/3	5+12+18	365+31?
B.M. No. 94.3.14.26	202+3+(4)15	38+38	2+5+12	4/3	5+11+16	325+31
B.M. No. 1930.1.27.177	202+4+(4)16	41−2+41	2+5+10	4/3	4+10+17	349+35
B.M. No. 1930.1.27.178	197+4+(4)16	40+45	2+4+10	4/3	4+11+17	333+32
B.M. No. 1956.1.16.28	200+4+(4)14	39−41+43	2+5+11	4/3	6+10+?	315+31
B.M. No. 1956.1.16.29	—+4+(5)16	—	2+4+10	4/3	5+ —	—
B.M. No. 1956.1.16.30	201+3+(4)x	42+45	2+5+11	4/3	6+12+18	233+x
I.M.Z.U.T. No. 969	197+4+(5)16	39+43	2+3+11	4/3	6+10+16	375+38
B.Y.U.C. No. 16124	202+4+(4)15	39+43	2+5+12	4/3	4+ 9+17	348+35
B.Y.U.C. No. 16127	195+4+(5)15	40+45	2+6+11	4/3	4+10+14	285+27
Z.S.M. No. 218/33	200+4+(4)16	37−8+42	2+5+12	4/3	6+10+18	368+34
B.M. No. 1928.1.8.13	198+4(4)18	33−4+34	2+6+13	4/3	4+10+17	253+29
C.N.H.M. No. 44134	214+4+(4)20	28−30+27−9	2+5+11	4/3	4+ 9+14	263+31
M.A.C.N. No. 90	211+3+(5)23	28−9+27−8	2+4+12	4/3	4+ 8+13	395+50
M.A.C.N. No. 17882	210+4+(5)23	32+31	2+4+11	4/3	4+ 9+16	153+20
S.M.F. No. 11814	208+4+(5)22	(61+—)	2+5+10	4/3	—	?135+18
D.Z. No. 6481	198+4+(4)16	34−7+42	2+6+12	4/3	4+14 —	383+37
C.M. No. 4531	193+4+(5)19	32+32	2+5+11	4/3	4+.8+12	327+37
C.M. No. 4532	195+4+(5)19	36+34	2+5+13	4/3	2−2+ 8+17	376+40
I.M.Z.U.T. No. 1907	209+4+(4)19	32+30	2+5+11	4/3	4+ 8+14	305+34?
S.M.F. No. 22099	212+3+(6)x	32+34	3(2)+5+11	4/3	4+ 8+11	328+x
S.M.F. No 28705	—	31−4+32−5	2+5+9	4/3	—	—
Z.S.M. No 219/33	213+4+(4)21	35+35−6	4+6+14	4/3	3F+10+5	200+27
Z.S.M. No. 221/33	217+2+(5)22	33+35	2+5+11	4/3	4+10+13	325+40
M.A.C.N. No. 2785	200+4(5)17	35+31−5	2+5+12	4/3	4+ 9+15	269+31
M.A.C.N. No. 3616	201+3+(4)17	32−4+28−30	2+3+12	4/3	2−2+ 7+14	351+42
Z.S.M. No. 222/33	194+4+(4)17	35+31	4+5+12	4/3	4+ 9+16	272+28
Z.S.M. No. 220/1933A	208+4+(4)19	32+35	2+5+12	4/3	4+ 9+14	236+28
Z.S.M. No. 220/1933B	213+4+(3)19	32+32	2+5+11	4/3	4+11+15	356+41
H.M. [Werner]	[201+23]	[30+30]	[2−—]	[4/3]	[4+6]	[330+35]
H.M. [Werner]	[195+22]	[32+28]	—	[4/3]	[4+6]	—

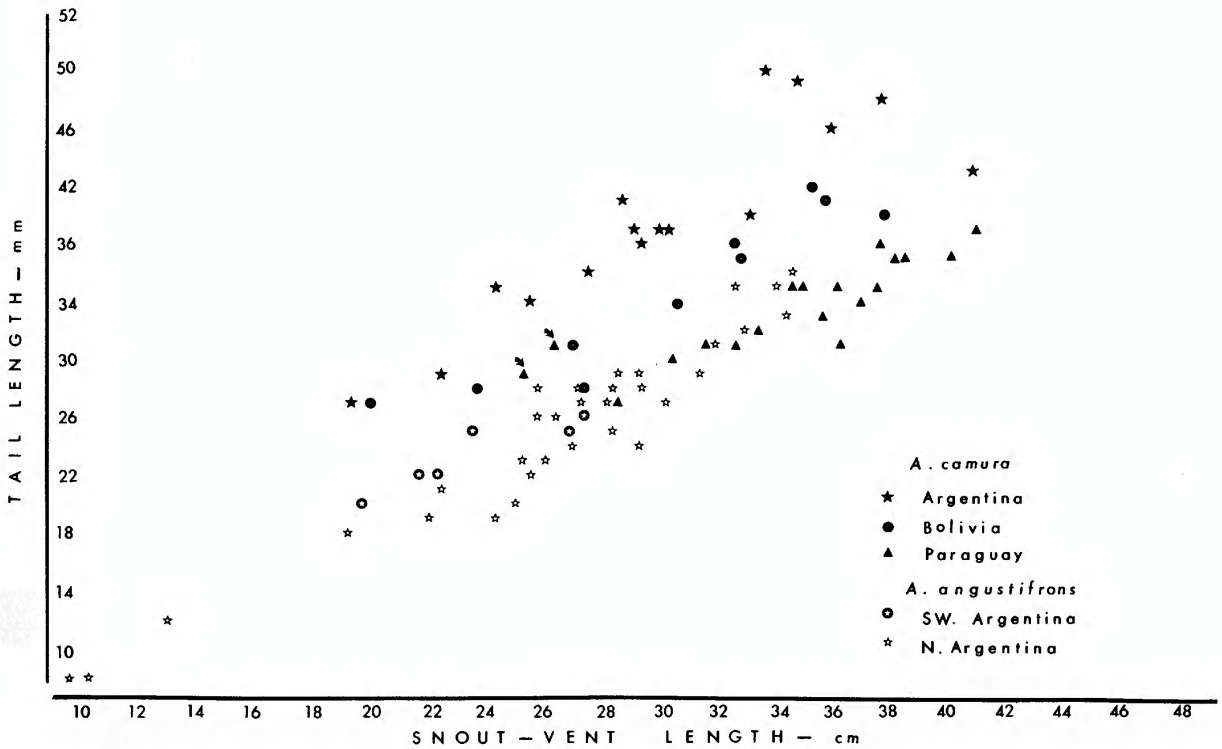

FIG. 2. *Amphisbaena*, scatter diagram of tail length versus snout-vent length for various samples. Arrows point to Paraguayan records from western portion of Paraguay to indicate that they fall with Bolivian specimens. Note that three specimens of *A. camura* from "Mato Grosso, Brazil," have been omitted, since they agree in all particulars with specimens of that species from Argentina (see text).

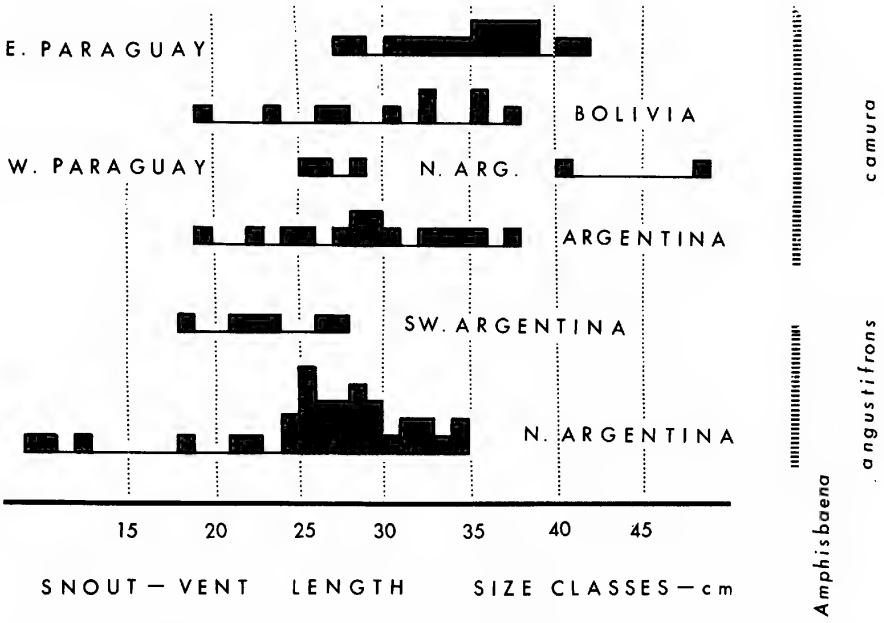

FIG. 3. *Amphisbaena,* histogram of snout-vent length for the various samples. Summation has been of values from the integer plus 0.05 up to and including the following integral value in each case (e.g., 17.05–18.00, 18.05 19.00). See caption for figure 2.

Pampa, Santa Fé, and Cordoba possess the maximum number of annuli among "typical" *angustifrons,* thus a La Pampa sample has a range from 210 to 223. The hiatus of more than 200 miles between the La Pampa site and the sites in Neuquén and Mendoza would not support conclusions regarding the reality of continuous variation. It is perhaps significant that all western specimens (including those from La Pampa) are somewhat smaller and lie in a single group on the scatter diagram of tail versus snout-vent length (fig. 2). Possibly they are sampled from a southeastern population of reduced size, with a higher number of annuli. The matter should be reconsidered when adequate samples become available.

The possible relationships of those southwestern specimens to a southwest Argentinian assemblage which has a high number of body annuli and medium number of midbody segments and is presently lumped under the name *A. plumbea* Gray (1872) remain to be investigated. This situation may be discussed in more detail in a subsequent paper.

GEOGRAPHIC VARIATION OF *Amphisbaena camura*

Amphisbaena camura shows far more geographic variation than does

A. angustifrons. The samples occupy a T-shaped geographic range, with central Argentina and Amazonian Bolivia forming the terminals of a wide horizontal bar and eastern Paraguay the end of a short vertical one. The data (table 2 and fig. 4) indicate that the terminal populations may be easily characterized by some five or more characters, including number of body annuli, mean numbers of dorsal and ventral segments to a midbody annulus, number of caudal annuli, site of autotomy level, relative tail length,[1] maximum size of adults, and pigmentation pattern on the head and neck.

The characteristics of the north Bolivian samples generally overlap or bridge the ranges of those of samples from Argentina and Paraguay. The single Brazilian specimen with a definite locality agrees with the characteristics of the Paraguayan sample; three other specimens marked only "Brazil" or "Mato Grosso" agree in all details with the Argentinian material and have hence been omitted from figures 2 and 4.

While the main groupings are indeed distinct, the differences between them are bridged by the ranges of the intermediate populations. The characteristics of samples from localities in central and western Paraguay, in the Bolivian state of Tarija, and in the Argentinian states of Salta, Jujuy, and Formosa either agree with those of one of the terminal populations, or are themselves distinct.

The samples from the intermediate zone are generally composed of but one or two specimens (per locality) and are thus inadequate for a proper mapping of the actual variation. Recognition of subspecies would represent a naming of the terminal points of clines. Concepts of the distribution of subspecies would depend upon the characters accorded most emphasis. Such nomenclatorial treatment would actually mask the interesting pattern of geographical variation. Therefore, I do not choose to apply subspecies names here.

KEY TO THE LARGE AMPHISBAENIDS OF SOUTHERN SOUTH AMERICA

Snout prognathous, with projecting, faintly spatulate rostral projecting beyond lower jaw; means of 20 to 31 dorsal and 21 to 30 ventral segments to a midbody annulus; 12 to 18 caudal annuli; tail conical, with a faint, vertical, terminal constriction and lacking autotomy; fourth supralabial generally split off posterior edge of third, with intermediate suture running posterodorsad from labial edge; segments most heavily pigmented on their anterior edge, this pigmented even on ventral segments, coloration more or less even

[1] One specimen, B.M. No. 1912.11.19.1, was omitted from figure 2 as it showed a relative tail length far greater than that of any other specimen. It was otherwise normal.

dorsally, lighter ventrally ..... *Amphisbaena angustifrons*
Snout less markedly prognathous, rostral tip more pointed, vertically oval, means of 28 to 42 dorsal and 27 to 46 ventral segments to a midbody annulus; 14 to 26 (17 to 26 in region of possible sympatry) caudal annuli, third, fourth, fifth, or sixth clearly narrowed as autotomy annulus; third and fourth supralabials parallelogrammic, with all sutures passing anterodorsad from labial edge; dorsal coloration even, segments uniformly colored, pigmentation fading along sides, ventral surface light; specimens generally with light-colored nuchal band, possibly obscure in adults (Bolivia), or extending as light-colored cap across entire head (south-central Argentina) ..... *Amphisbaena camura*

Amphisbaena angustifrons Cope

Amphisbaena angustifrons COPE, 1861, p. 76. Terra typica: "Buenos Ayres," Argentina. Holotype: A.N.S.P. No. 9690.

Amphisbaena knighti PARKER, 1928, p. 383. Terra typica: "Bonifacio, Argentina (approx. 36° 18′ W)." Holotype: B.M. No. 1928.5.2.1-RR1946.8.31.76. Paratypes: B.M. No. 1927.5.26.4 (Bonifacio); B.M. Nos. 1909.11.2.8-RR1946.8.8.71–1909.11.2.9-RR1946.8.8.72 (Ajo, Prov. Buenos Aires); B.M. No. 1902.7.29.65 (Tucumán).

DIAGNOSIS: A medium to large-sized species of *Amphisbaena,* with the post-rostral head shields paired and without major fusions of head shields; with an elongate, acutely pointed head, terminating in a narrow, faintly spatulate tip, and with a short, conically reduced tail that lacks an autotomy annulus and cannot be autotomized. Specimens have 190 to 215 (occasionally to 253) body annuli; 12 to 18 caudal annuli; and means of 20 to 31 dorsal and 21 to 30 ventral segments to a midbody annulus. Four, rarely three, five, or six precloacal pores. Living specimens brownish above, lighter below, with reddish purple overtones. Pigmentation appearing concentrated along anterior portions of segments which are otherwise evenly colored.

DESCRIPTION: The characteristics of the Mendoza, La Pampa, and Neuquén specimens are given in parentheses when they differ from those of the rest of the material. Meristic characters are summarized in table 1. Figure 5 shows views of the head; figure 6, the ventral surface of the tail; and figures 7, 8, 9, and 10 show photographs of segment proportions and pattern details. Figures 2 and 3 show relative tail length and size variation.

This is a medium to large, robust species of *Amphisbaena,* in life of uniform dark brown dorsal and somewhat lighter ventral coloration. The segmental pigmentation is uniform except for the marked increase in its density on the anterior part of each segment. Countershading occurs by the fading out of the pigment on the posterior half of a segment, and the differential becomes more noticeable on preserved specimens. The rostral

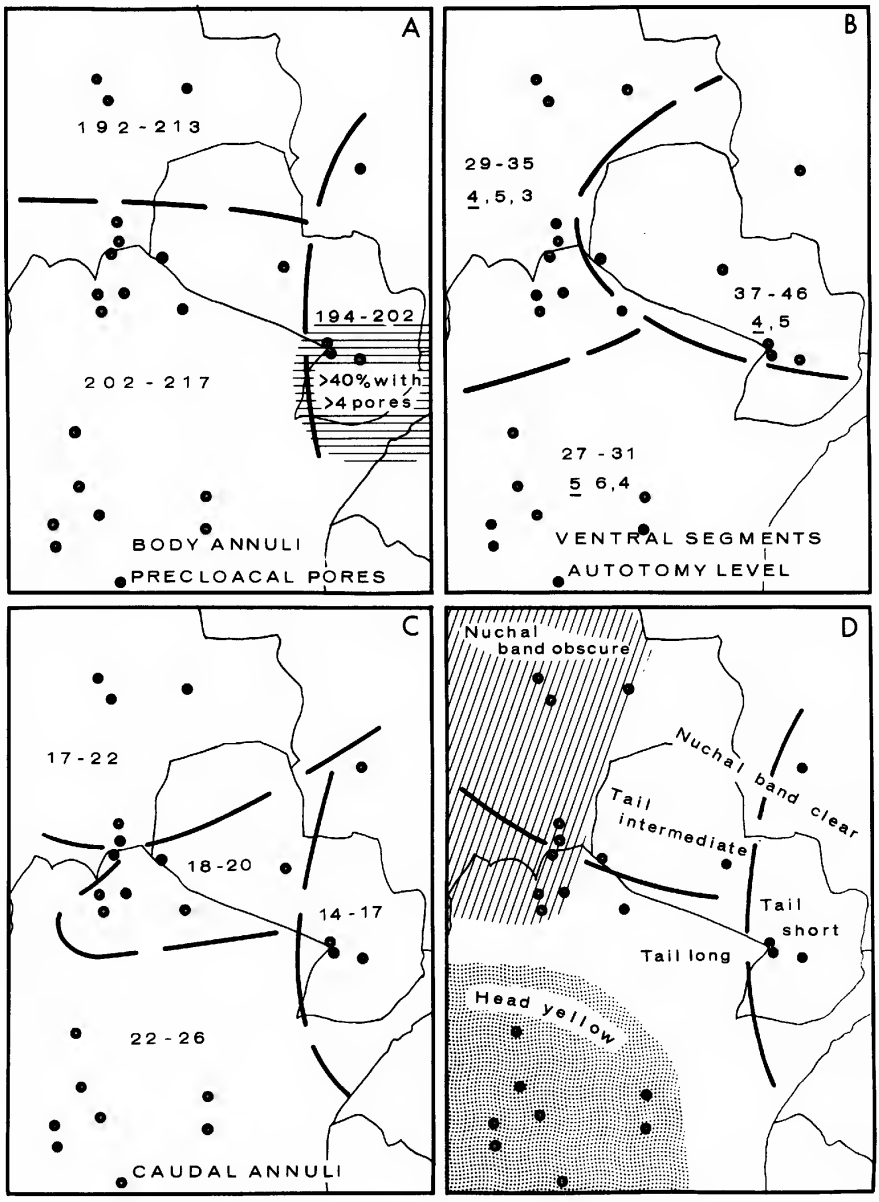

FIG. 4. *Amphisbaena camura,* summary of geographic variation. A. Body annuli and frequency of precloacal pore number greater than 4. B. Distribution patterns for ranges of range midpoints of numbers of ventral segments to a midbody annulus and site of autotomy level (mode underlined followed by other classes in order of frequency). C. Number of caudal annuli (ranges). D. Relative tail length (compare fig. 2) and nature of coloration of the head. Specimens of the eastern part of the range have the nuchal band more or less clearly marked, those in the northwest show this obscured, particularly in large adults, while specimens in the southwestern region have the entire head colored yellow.

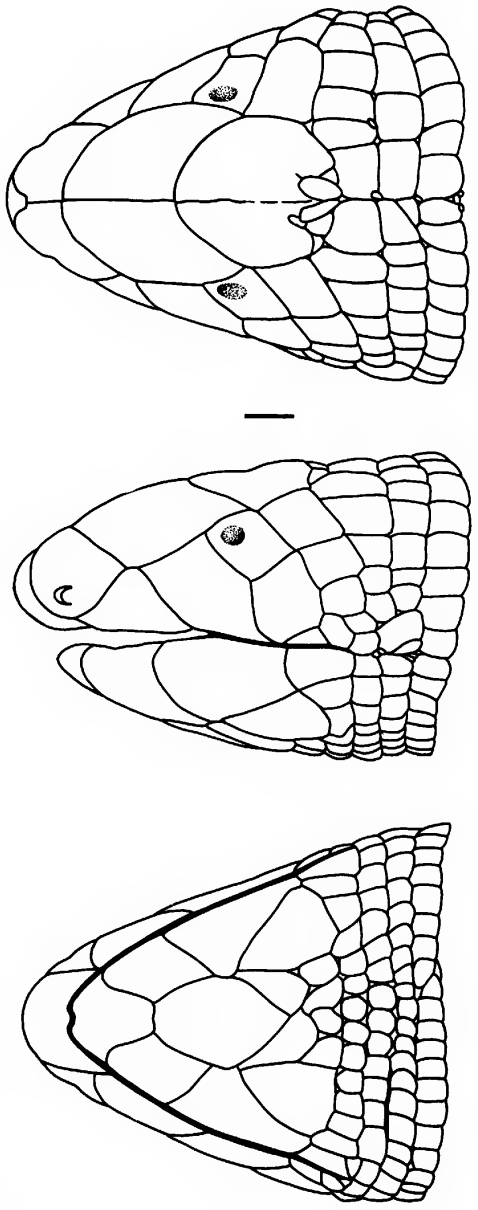

FIG. 5. *Amphisbaena angustifrons*, dorsal, lateral, and ventral views of the head of the holotype, A.N.S.P. 9690, from Buenos Aires, Argentina. The line equals 1 mm. to scale. Drawn by Virginia Cummings.

tip, the ventral part of the supralabials, and the middle of the chin shields are light colored in life and bleach to white in preservatives. The ventral countershading is less marked along the first tenth of the body and beneath the tail.

The head segments show no major fusions. The middorsal segments of the first rows following the frontals are of regular size, without significant enlargement. The head is pointed and slopes in a straight line at an acute angle toward the rostral tip, which is faintly spatulate horizontally, much like a horizontally cylindrical swollen edge. This slope is covered by the enlarged nasal, prefrontal, and frontal shields. The rostral edge and the anterior portion of these shields often give the impression of a faintly keratinized surface. The head is somewhat smaller than the trunk, set off slightly by the reduction of the nape posterior to the bulging temporal muscles. The nuchal region widens markedly at the level of the twentieth to thirtieth body annulus where the trunk achieves its greatest diameter. The trunk is subcylindrical in cross section and shows slight horizontal compression.

In size the rostral is approximately equal to the first supralabial, these segments sharing a very short common suture. In dorsal view the rostral appears as a tiny triangle, if at all. Ventrally, it covers an area greater than that of the mental. Pairs of large nasals, much larger prefrontals, and smaller frontals follow in sequence along the dorsal midline of the head. The frontals may be divided by a pair of sutures that form a posteriorly acute angle with the midline. Various modifications occur, and some specimens have the sutures which end blindly in the frontals. The dorsal segments of the first body annulus may be slightly enlarged, but never sufficiently to be considered parietals. The frontals thus extend posteriorly to a level anterior to the start of the temporal bulges, which is equivalent to the middle of the third supralabial.

There are four, rarely three, supralabials, the second the largest, the first, third, and fourth following in order of size. The fourth supralabial is generally a small, triangular segment cut off from the third; in cases in which only three supralabials are present, the suture is interrupted. Occasionally, as in one side of the holotype, the third supralabial is split by an ascending suture that divides off a wedge-shaped labial segment from the main portion of the shield. The first, second, and third interlabial sutures run anterodorsad at angles of 30 degrees, 45 degrees, and 45 degrees, respectively, to the labial edge. The fourth suture runs posterodorsad at 60 degrees. The ocular is more or less rectangular and is in contact with the second and third supralabials and prefrontal. It is in point contact with the frontal and in posterior contact with one or two enlarged segments of the first body annulus. The eye is large and clearly apparent.

The lower jaw is fairly shallow and inserted within the prognathous snout. The mental is relatively small, flanked on each side by the some-

what larger first infralabials which enclose the anterior aspect of the larger pentagonal postmental. The second of the three infralabials is by far the largest (its medial tip is separated by a suture in some specimens); the third is the smallest. The malars are subtriangular, generally equivalent in area to the first infralabials, but of varying proportions. A pair of large drop-shaped or halfmoon-shaped segments of the first postgenial row surrounds the posterior aspect of the postmental, keeping it from contact with the malars. An occasionally enlarged median segment of the first postgenial row in some cases projects to touch the postmental on the midline. The second postgenial row consists of two to four small central segments, flanked on each side by equivalent-sized ones, giving the impression that they were cut off the posteromedial corners of the malars. Thus the total row numbers from four to seven, normally five, segments, of which the ventral one is often enlarged. The row is lacking in some of the specimens (including all three from Esquina Grande, Catamarca). The post-malar row contains nine to 14, normally 10 or 11, more or less regular, small segments.

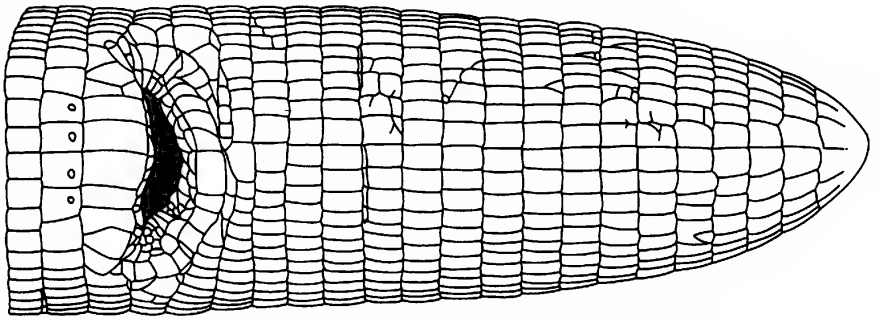

FIG. 6. *Amphisbaena angustifrons,* ventral view of the tail of the holotype, A.N.S.P. 9690, from Buenos Aires, Argentina. The line equals 1 mm. to scale. Drawn by Virginia Cummings.

Dorsally the first body annulus sweeps forward to include the two enlarged, roughly rectangular segments, formerly referred to as temporal and postocular. A few specimens from the southwest have the postmalar row continuing dorsad to include the fourth supralabial, temporals, and postocular. There are one to two dorsal, intercalated half-annuli in the nuchal region. These are generally inserted between the first and second and the second and third body annuli. The suture be-

FIG. 7. *Amphisbaena angustifrons,* dorsal, lateral, and ventral views of the head of M.A.C.N. 4403 from Buenos Aires, Argentina, to show scale proportions.

tween the third and fourth body annuli passes vertically; all anterior ones incline anterodorsad. The midventral segments of the first six to eight body annuli are smaller and rounded, forming a more or less flexible throat region that appears concave in most preserved specimens. Some specimens show the twentieth to fiftieth annuli in a smooth, somewhat posteriorly concave curve in dorsal view.

FIG. 8. *Amphisbaena angustifrons,* anterior three-quarters view of the head of I.M.L. No. 143 from Buenos Aires, Argentina, to show the bulging temple muscle masses, the straight passage of the shield-covered plane, and its termination in a narrow, spadelike process.

There are 190 to 215 (210 to 253) body annuli from the level of the angulus oris up to and including the pore-bearing precloacals. There are 20 to 31 dorsal and 20 to 30 (means of 21 to 30) ventral segments to a midbody annulus. The variation here is remarkable in that there may be a difference of two to three between adjacent annuli. The dorsal surface also bears varied diagonal folding lines that cross the segments for varying distances. The dorsal segments are incompletely rectangular, and tiny equilateral triangular segments interdigitate between them on

FIG. 9. *Amphisbaena angustifrons,* dorsal and ventral views at midbody of I.M.L. No. 148 from Capital, Tucumán, to show segment proportions and segmentation. The pattern here is unusually irregular.

their posterior sutures, and there are traces of very tiny segments in the sutures of body annuli.

The cloacal region is characterized by three to six (usually four) small, round, precloacal pores found even in juveniles and females, six to 10 precloacal segments, of which the six central ones are by far the largest, and 12 to 20 postcloacals, of which only the central pair is widened. The cloacal region corresponds to three to four, rarely and asymmetrically two, lateral annuli. It is followed by one to three, often rather narrow, postcloacal annuli which are the first of a total series of 12 to 18 (16 to 18) caudal annuli that extends to the vertically oval caudal tip. There is no trace of an autotomy annulus; none of the specimens had an autotomized tail, and the tail of the living specimen would not autotomize. In section the tail appears ventrally flattened, dorsally curved, and wider than high, except for the distal tip which has a vertically oval cross section.

The lateral sulci are clearly marked after approximately the thirty-fifth body annulus and continue up to the level of the cloaca. They are as wide as or wider than a bordering segment and filled with irregularly

FIG. 10. *Amphisbaena angustifrons,* lateral and ventral views of cloaca and tail of C.M. No. 38031, to show propositions of tail and absence of autotomy plane.

shaped segmental fragments. There is barely a trace of a dorsal sulcus, and, where present, it is expressed as an alignment of intersegmental sutures. The ventral sulcus is similarly indicated.

The middorsal segments are one and three-quarters to two times as long as wide. The midventral segments are wider than long, but there is marked size variability from annulus to annulus and even from side to side.

DISTRIBUTION RECORDS: URUGUAY: "Montevideo," M.S.N.G. No. CE—.

ARGENTINA: —, M.A.C.N. No. 4166. *Misiones:* —, M.A.C.N. No. 3760. *Buenos Aires:* —, M.A.C.N. Nos. 17843, 17856, 17859, 17879, 17881. Ajo (Parker, 1928); B.M. Nos. RR1946.8.8.81–RR1946.8.8.72 (paratypes of *knighti*). Buenos Aires (Cope, 1861, 1885); A.M.N.H. Nos. 17023, 65190; A.N.S.P. No. 9690 (holotype of *angustifrons*); M.A.C.N. No. 6903. Buenos Aires, vicinity of, M.S.N.G. No. 29010. Bonifascio (Parker, 1928); B.M. Nos. RR1946.8.31.76 (holotype of *knighti*), 1927.5.26.4 (paratype of *knighti*). La Pampa: La Primavera, department of Santa Rosa, M.A.C.N.

Nos. 7916–7918. *Neuquén:* Auca Mahuida, M.A.C.N. No. 7976. Plothier, M.A.C.N. No. 10262. *Mendoza:* Mendoza, M.A.C.N. No. 17878. *Entre Rios:* —, H.M. No. 595, *Santa Fé:* Santa Fé (*ex* La Plata), U.S.N.M. No. 22764. Bañados del Rincon, C.M. No. 38031. *Cordoba:* —, H.M. No. 5220. Cordoba, M.A.C.N. No. 17875. La Laguna, M.A.C.N. No. 4346. *Catamarca:* Andalagalá, M.A.C.N. No. 3586. Esquina Grande, M.A.C.N. Nos. 10893–10895. *Tucumán:* Tucumán (Parker, 1928); B.M. No. 1902.7.29.65 (paratype of *knighti*); I.M.L. No. 148; I.M.Z.U.T. No. 967–A; M.A.C.N. No. 17860. Ciudadela, I.M.L. No. 245. Villa Padre Monti, Burruyacú, I.M.L. No. 199. Valle del Río Cochuna, El Petrerillo, I.M.L. unnumbered. *Chaco:* —, M.A.C.N. No. 17857. *Salta:* Urundal, I.M.L. No. 143.

Bolivia: *Tarija:* Upper Pilcomayo, near Villa Montez, Z.S.M. No. 228/33.

Amphisbaena camura Cope

Amphisbaena camura Cope, 1862, p. 350. Terra typica: "Paraguay" = "Ascunción, Paraguay," by present restriction. Syntypes: U.S.N.M. No. 5860 (2 specimens).

Amphisbaena boliviana Werner, 1910, p. 35. Terra typica: "Prov. Beni, Bolivia, Quellgebiet des Amazonas." Syntypes: Formerly H.M.; destroyed.

Amphisbaena camura bolivica Mertens, 1929, p. 60. Terra typica: "Villa Montes, Rio Pilcomayo, Süd Bolivien." Holotype: S.M.F. No. 22099. Paratype: S.M.F. No. 28705, anterior half only.

Diagnosis: A large-sized species of *Amphisbaena* with postrostral head shields paired, and without major fusions of head shields; with a short pointed head terminating in a rounded vertically oval tip; and with a relatively short, terminally rounded tail. Specimens having 194 to 217 body annuli; 14 to 26 caudal annuli; an autotomy annulus generally at fourth or fifth caudal; means of 28 to 42 dorsal and 27 to 45 ventral segments to a midbody annulus. Generally four to six precloacal pores or pore scars. Specimens brown above, lighter below, with segments pigmented uniformly and color gradually fading out along sides. Specimens having a light-colored nuchal band that may in some populations be obscured in adults or extended to cover snout. Meristic, size, and pattern characters showing marked geographic variation within above limits (cf. figs. 2, 3, and 4).

Description: Meristic characters are summarized in table 2. Figure 11 shows views of the head; figure 12, the ventral surface of the cloaca and tail; and figures 13 to 16 show photographs of segment proportions and pattern details. Figures 2 and 3 show relative tail length and size variation, and figure 4 summarizes geographical variation of characters.

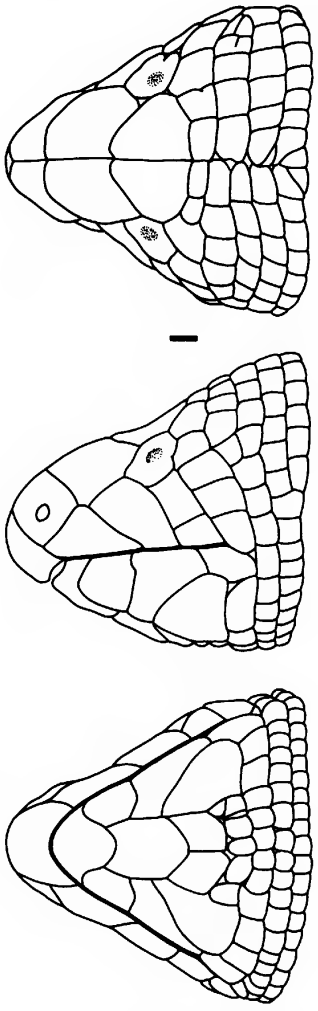

FIG. 11. *Amphisbaena camura,* dorsal, lateral, and ventral views of Z.S.M. No. 223/33, to show segment proportion. The line equals 1 mm. to scale. Drawn by Virginia Cummings.

This is a large, robust species of *Amphisbaena,* in life of a uniform light brown dorsal and a clear whitish ventral coloration. The segmental pigmentation is uniform across each segment, with a faint accentuation of the anterior edge. It fades out evenly along the sides. The intersegmental raphes are lighter colored. The dorsal coloration extends in a triangular tip into the nuchal region, terminating near the level of the first body annulus. Along the sides the pigment markings curve back in a more or less regular fashion to the level of the third body annulus. The snout is often pigmented across all enlarged shields, giving the appearance of a light nuchal collar or band in some populations (fig. 4D). Other specimens show this symmetrically. When dark pigment is lacking on the

head, the rostral, nasal, prefrontal, and frontal shields tend to be colored somewhat more deeply, suggesting a thickened epidermis. The ventral countershading extends from the tip of the lower jaw to that of the tail. The autotomy annulus is not emphasized by pigmentation.

The head segments show no major fusions. The middorsal segments of the first rows following the frontals are of regular size, without significant enlargement. The head is pointed, and the rounded rostral tip forms a vertical oval. The sagittal profile curves backward convexly to the level of the prefrontal-frontal suture and becomes faintly concave along the frontal; thereafter, it curves more sharply concave and then broadly convex onto the striking, bulging temporal muscle masses, between which the sagittal line tends to form a groove. The head is slightly smaller than

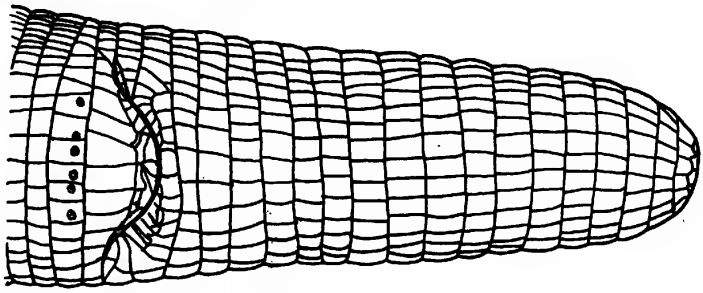

FIG. 12. *Amphisbaena camura,* ventral view of cloaca and tail of U.S.N.M. No. 5860B, syntype of *A. camura,* from "Paraguay."

the trunk, and there is no significant nuchal constriction. Maximum trunk diameter occurs at one-eighth to one-tenth of the over-all snout-vent length beyond the tip of the snout, and the transition is straight line. The trunk is subcylindrical, almost circular, in cross section and shows but traces of horizontal compression in some specimens.

The rostral is slightly larger than the first supralabial, but only a point of it appears in dorsal view, while its area ventral view is approximately equal to that of the mental. Pairs of large nasals, slightly larger prefrontals, and smaller frontals follow in sequence along the dorsal midline of the head. The frontals occasionally show some modification along their posterior edge, or they may be split longitudinally into an inner and outer pair. The segments of the first four dorsal half-annuli are slightly wider than those of the succeeding ones, but there are no enlarged parietals. The frontal extends posteriorly, slightly beyond the beginning of the temporal bulges, a position equivalent to the middle of the first supralabials. In large specimens the dorsal midline is represented by a deeply

inserted fold, commencing from the back of the frontals and extending past the temporal bulges and onto approximately the tenth body annulus.

There are four supralabials; the first has the longest exposure along the jaw; the second is the tallest. The size of the third varies, since it may be subdivided to form a subocular. The fourth supralabial is the smallest of the series, but is more or less rectangular; it forms part of the last annulus anterior to the angulus oris. The interlabial sutures run anterodorsad at angles of 30 degrees, 30 degrees, 45 degrees, 50 degrees, and 45 degrees to the labial edge. The ocular is pentagonal and is in contact with the second and third supralabials (or infraocular), with the frontal and prefrontal, and with two regular-sized segments of the postocular row. The ocular may be subdivided in various patterns, particularly since the folding line from the bulging temporal muscles passes across it. The eye is large and clearly apparent.

The lower jaw is relatively deep and slightly inserted beneath the snout. Infralabials and malars thus have greater lateral than ventral projection area. The medium-sized mental is rounded in ventral view. It is followed by three infralabials, the large second sending a process anteroventrad to touch the medium-sized, more or less pentagonal postmental. The latter is concave anteriorly. The first and third infralabials are next in order of size. The malars are generally wider than long and in extended point contact with the postmentals. The lateral tips of one or both malars are occasionally separated into a distinct segment, which keeps the malar proper from contact with the infralabials. The mental is in almost every case followed by two large, squarish segments of the first postgenial row; these in turn are followed three to six much smaller and irregularly shaped segments of the second postgenial row. The lateralmost of these appears to have divided off the posteromedial corners of the malars. The postmalar row contains nine to 14 segments, the lateral ones often slightly widened.

Dorsally, the postmalar row corresponds to a half-annulus that includes the supralabial, a varying number of small temporal and postocular segments, and, in some specimens, a group of segments that join behind the frontal. The first two body annuli curve forward slightly. There are one to two intercalated dorsal half-annuli within this region, apparently induced less as compensation for anterior forward curvature than by the need to cover the notably bulging temporal muscle masses. The third (fourth) body annulus passes vertically. The first through sixth annuli are somewhat narrower, particularly in the ventral region where they, and often some of the following annuli, form a variable pattern of rounded segments.

FIG. 13. *Amphisbaena camura,* dorsal, lateral, and ventral views of the head of the syntype, U.S.N.M. No. 5860B, from "Paraguay." Note the relatively short, shield-covered portion and the marked swelling of the temporal muscle masses.

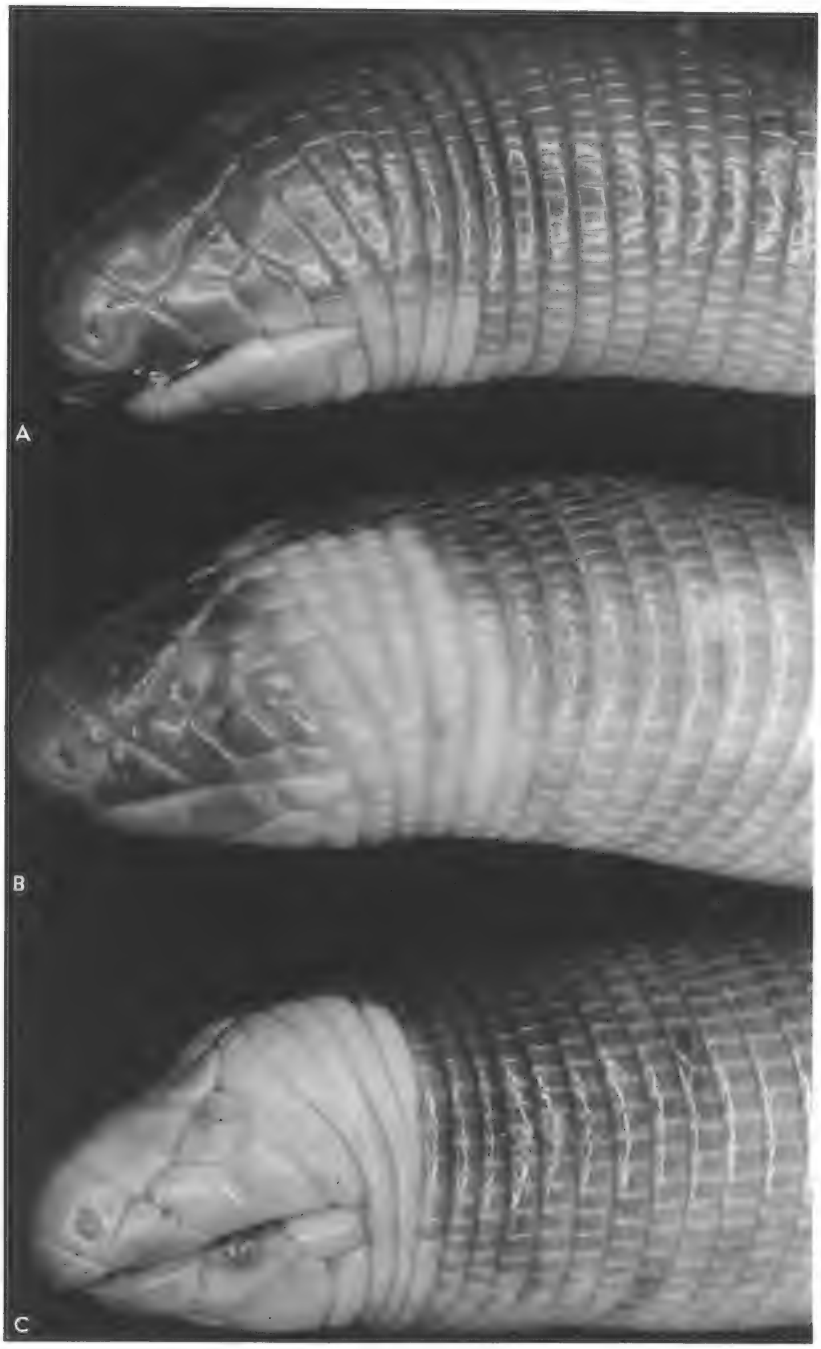

FIG. 14. *Amphisbaena camura,* three-quarter frontal views of three specimens to show appearance of snout and nuchal color pattern. A. I.M.L. No. 237 from Hickman, Salta. This specimen has the nuchal region obscured. B. A.M.N.H. No. 25173 from Villa Rica, Paraguay. This specimen shows a regular light nuchal band. C. Z.S.M. No. 223/33 from La Geraldina, Santa Fé, Argentina, shows an entirely lightened head.

FIG. 15. *Amphisbaena camura,* dorsal and ventral views at midbody of Z.S.M. No. 223/33, from La Geraldina, Santa Fé, Argentina, to show relative segment proportions and the herringbone appearance of the dorsal segments.

There are 194 to 217 body annuli from the level of the angulus oris up to and including the pore-bearing precloacal row. There are 28 to 45 (means of 28 to 42) dorsal, and 27 to 45 ventral, segments to a midbody annulus. The variation here is extremely marked, and there is scarcely any alignment of intersegmental sutures from annulus to annulus. A middorsal view shows that the segments are not truly rectangular, but are arranged in a faint herringbone pattern at a posteriorly open angle of some 5 degrees to the midline; the functional significance of this arrangement bears investigation. The dorsal surface bears varied diagonal folding lines of major and minor extent. On poorly preserved specimens the stretched skin shows some small segmental fragments along the interannular raphes.

The cloacal region is characterized by four or six, rarely three or five, small, round, precloacal pores. In juveniles and females these are generally expressed as pore scars, blind-ended sutures running from the segmental center to its posterior margin, and lacking any core. A very few specimens have two short rows of pores separated by one or two regular

segments; in one specimen two pores were on a single enlarged segment. This row is followed by a "segment-shaped" precloacal shield bearing eight to 12 segments, of which eight or more tend to be enlarged. The posterior margin of the cloaca is formed by 12 to 20 segments, of which the two central ones are enlarged. The lateral segments are arranged parallel to the interannular sutures. The cloacal region corresponds to four, occasionally three, lateral annuli.

The cloacal region is followed by one or two narrow post-cloacal annuli which form the first of a series of 14 to 26 caudal annuli which extend up

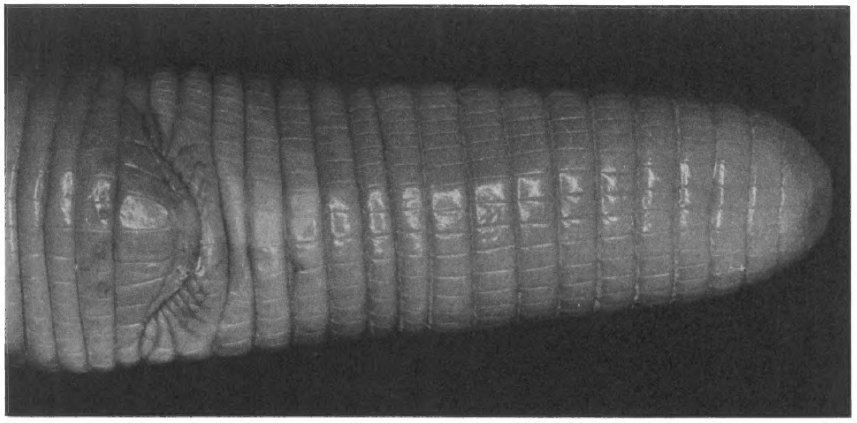

FIG. 16. *Amphisbaena camura,* ventral view of cloaca and tail of the syntype, U.S.N.M. 5860B.

to the distally rounded caudal tip. The segments covering the tip are not set off by deep raphes but form an arrangement of inscribed lines on a smooth hemisphere. The third, fourth, or fifth caudal annulus is markedly narrowed and serves as the autotomy site. Almost 10 per cent of the specimens have tails broken at this point. Anterior to the autotomy annulus the tail appears ventrally flattened; beyond the constriction it assumes a circular cross section. In general the tail is of much smaller diameter than the trunk, particularly noticeable in the short-tailed populations.

The lateral sulci are clearly marked after about the fortieth annulus and continue up to the fifth precloacal annulus. At midbody, they are as wide as one and one-half bordering segments and are filled with irregularly shaped segmental fragments. There is neither a dorsal sulcus nor an alignment of intersegmental sutures, though a ventral sulcus is expressed by sutural alignment.

The middorsal segments are more than twice as long as wide; the midventral segments range from somewhat longer than wide to somewhat wider than long.

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PARAGUAY: — (Cope, 1862); M.A.C.N. No. 17855; N.M.B. No. 3812; U.S.N.M. Nos. 5860A–5860B (syntypes of *camura*); V. M. No. 12329. Villarica (Burt and Burt, 1931); A.M.N.H. No. 25173. Colonia Nueva Italia, C.N.H.M. No. 42292. Asunción (Boulenger, 1894a; Peracca, 1895); B.M. Nos. 94.3.14.23–94.3.14.26, 1930.11.27.177–1930.11.27.178, 1956.1.16.28–1956.1.16.30; I.M.Z.U.T. No. 969. Asunción, streets of, B.Y.U.C. Nos. 16124, 16127. Asunción, Jardin Botanico (Hellmich, 1960); Z.S.M. No. 218/33. Makthlawaika (25° 25′ S., 58° 19′ W.), B.M. No. 1928.1.8.13. Fortín Guachalla, on Río Pilcomayo (Choco), C.N.H.M. No. 44134.

BRAZIL: *Mato Grosso:* —, M.A.C.N. Nos. 90, 17882; S.M.F. No. 11814. Taunay, D.Z. No. 6481.

BOLIVIA: —, C.M. Nos. 4531–4532. *Tarija:* Caiza (= Villa Ingavi), (Peracca, 1897; Mertens, 1929); I.M.Z.U.T. No. 1907. Villa Montes (Mertens, 1929; Hellmich, 1960); S.M.F. Nos. 22099 (holotype of *bolivica*), 28705 (paratype of *bolivica*); Z.S.M. Nos. 219/33, 221/33. *Santa Cruz:* Santa Cruz de La Sierra, M.A.C.N. Nos. 2785, 3616. San José de Chiquitos (Hellmich, 1960); Z.S.M. No. 222/33. Buenavista (Hellmich, 1960); Z.S.M. Nos. 220/1933A–220/1933B. *Beni:* — (Werner, 1910); H.M. (syntypes of *boliviana;* lost).

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